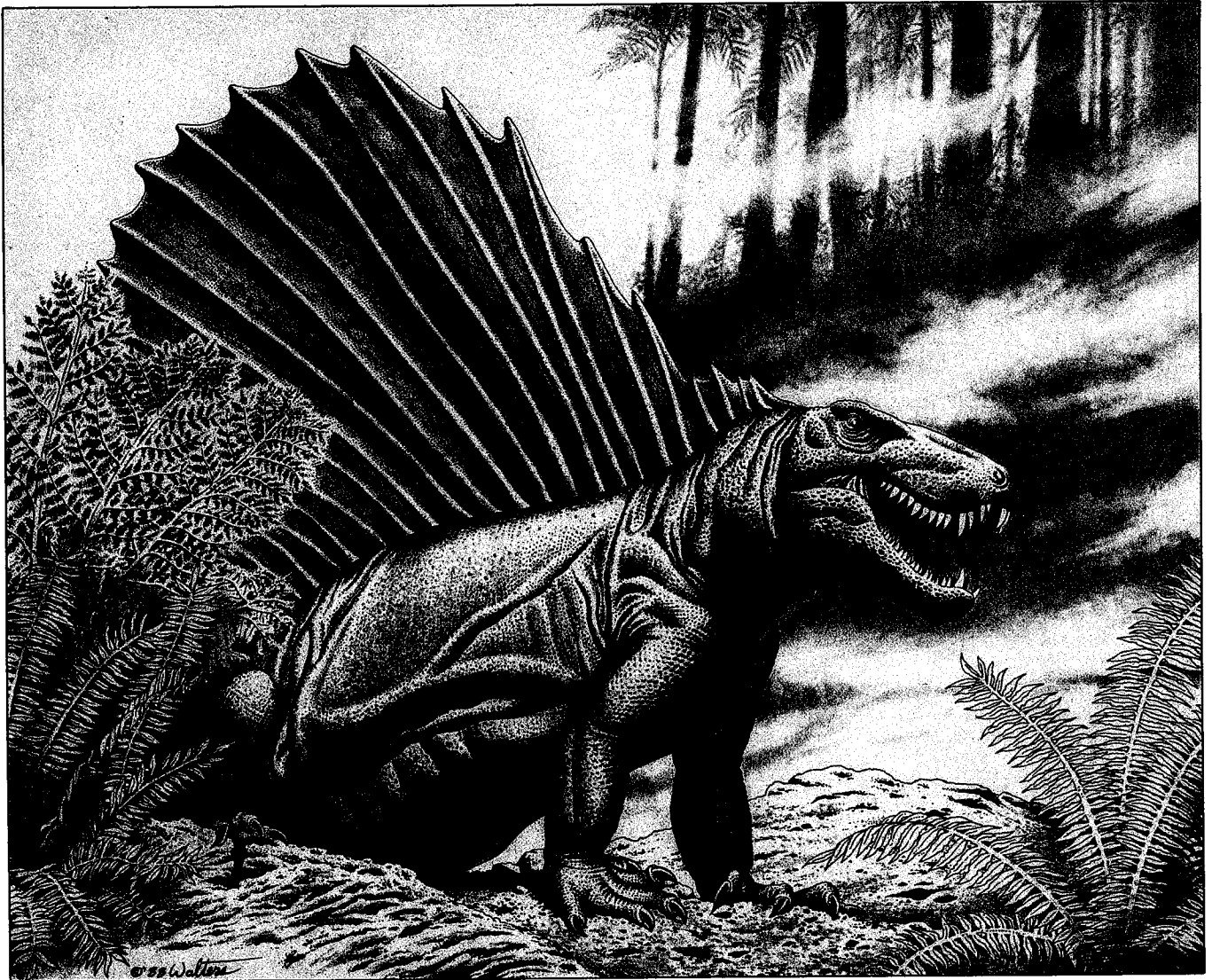


THE MOSASAUR



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The Mosasaur

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The Vertebrate Fauna from the Judith River Formation (Late Cretaceous) of Wheatland and Golden Valley Counties, Montana

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Abstract

Recent paleontological exploration of the Judith River Formation (Late Cretaceous) of south-central Montana has yielded a diverse vertebrate fauna which includes the remains of such animals as fish, crocodiles, turtles, pterosaurs, dinosaurs, and mammals. Approximately 3,000 fossil vertebrate specimens have been collected in this region as a result of these explorations. Paleogeographic reconstructions of the Upper Cretaceous of central North America place an inland sea to the east of this study area while to the west lay tectonically active highlands. Since the quarries discussed here are arranged along an east-west transect they provide a means by which to sample along an ecological gradient representing a more marine facies to the east and a more terrestrial facies to the west. Results of this study show that a marked increase in both the number of marine fish taxa and the relative abundance of these taxa exists in the easternmost quarry compared to the more western quarries. This difference in eastern and western faunas is not reflected among the more terrestrial faunal elements such as the dinosaurs. Presumably this is the result of these latter elements not being influenced by the effects of a largely aquatic ecological gradient.

Introduction

A new dinosaur-producing fossil field in the Judith River Formation of south-central Montana is currently being developed by field parties from the Academy of Natural Sciences of Philadelphia and the University of Pennsylvania. Since the initial discovery of Careless Creek Quarry by Eddy Cole in 1981, Academy/University field parties have continued excavating in this quarry and have located several additional quarries from four local sections in the surrounding area (Figure 1). The six quarries discussed in this report are located in easternmost Wheatland County and western Golden Valley Counties, within the Musselshell River Valley of Montana.

The discoveries from these quarries have already provided many interesting results. The first new ceratopsid to be described in 35 years, for example, was recovered from Careless Creek Quarry (*Avaceratops lammersi* Dodson, 1986), while this same quarry has also produced an abundance of juvenile dinosaurs (Fiorillo, 1987a). This latter example helps refute the view that dinosaurs nested exclusively in upland regions (e.g., Horner, 1984). These new quarries have also provided new

perspectives on taphonomic problems. One site, Antelope Head Quarry (Fiorillo, 1987b), has shown that shallow sub-parallel sets of scratch marks on bone surfaces are not a valid criterion for determining hominid carcass utilization behavior (e.g., Shipman & Rose, 1983) by demonstrating these features on dinosaur bones. Alternative causes for these scratch marks, such as trampling, must be explored when these features are encountered (Fiorillo, 1984, 1987b, in press). A taphonomic examination of Careless Creek Quarry has suggested that trapping mechanisms may be critical to the formation of quarry concentrations of bones within active channel environments (Fiorillo, in preparation). For Careless Creek Quarry, this mechanism was a log jam. This report reviews the fauna recovered from these excavations as a whole in terms of the variations in composition at each quarry and highlights the faunal differences between quarries.

Throughout this paper, catalogue numbers for cited specimens held at the Academy of Natural Sciences of Philadelphia are preceded by the acronym ANSP.

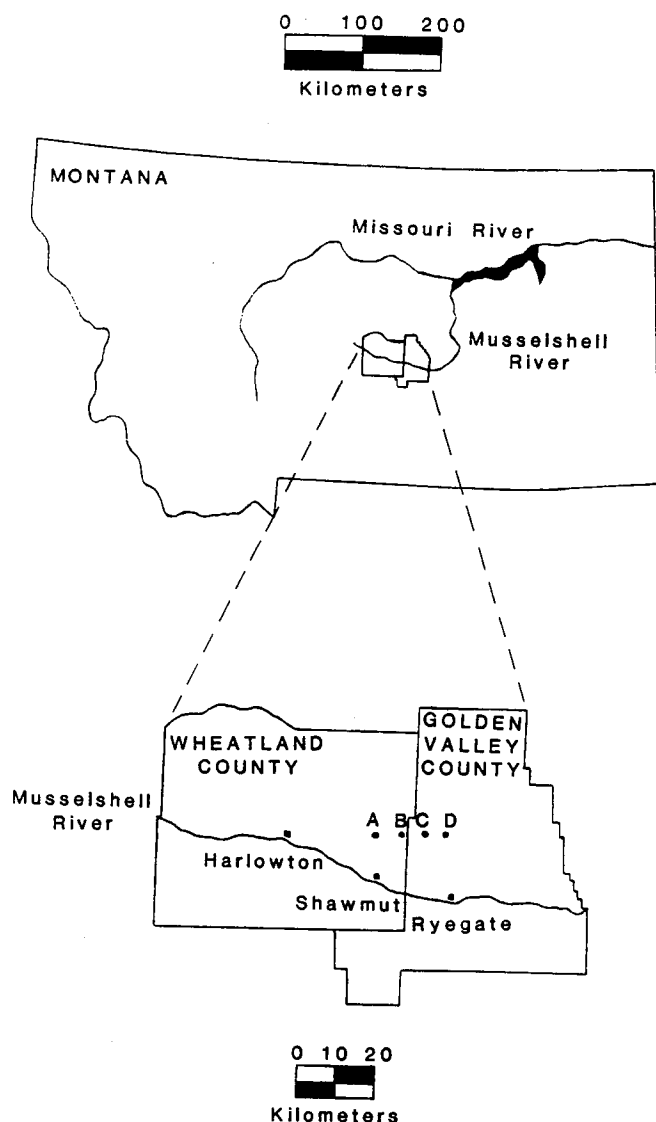


Figure 1. Location of stratigraphic sections containing new Judith River Formation quarries in Wheatland and Golden Valley Counties. The location of each section is designated by the letter A, B, C, or D. The corresponding sections are given in Figure 2.

Geologic Setting

Stratigraphically, these quarries are located in the Judith River Formation, a unit which is found at the surface or in the sub-surface of much of central and northern Montana and southern Alberta. These quarries are located in southern Montana, within the southernmost exposures of this unit. The Judith River Formation of southern Alberta has long been recognized as producing one of the richest dinosaur faunas in the world (e.g., Dodson, 1971, 1983), while in central Montana the formation is credited with producing the first dinosaur remains from North America (Leidy, 1856).

The age of the formation is currently under debate. Traditionally, this formation has been considered to be Campanian in age, based largely on correlation with ammonite zones (e.g., Gill & Cobban, 1973). More recently, it has been suggested that the formation may in fact straddle the Campanian-Maastrichtian boundary and a Judithian Age was suggested for the faunas of the Judith River based on terrestrial mammal remains (Lillegraven & McKenna, 1986). The formation, however, remains unequivocally in the Upper Cretaceous. Regionally, the marine Claggett Formation underlies the Judith River Formation while overlying this unit is the marine Bearpaw Formation. To the east the Judith River Formation grades into the marine Pierre Shale.

The Judith River Formation consists largely of non-marine sedimentary rocks representing a suite of fluvial and paludal depositional environments. These rocks accumulated on an aggrading coastal plain dominated by fluvial sedimentation which lay between alluvial fans in the west and the Western Interior Seaway to the east (Eisbacher et al., 1974).

The six quarries which provided the faunal data discussed in this report are exclusively from fluvial facies of this non-marine sequence and are arranged along an east-west transect approximately 25 km long (Figures 1, 2). Three quarries (Careless Creek Quarry [CCQ], Hidden Valley Quarry [HVQ], and Karen's Quarry [KQ]) are from channel facies while the remaining three quarries (Top Cat Quarry [TCQ], Antelope Head Quarry [AHQ], and SPA Quarry [SPAQ]) are from overbank deposits. Detailed examinations of Careless Creek Quarry (Fiorillo, in preparation) has shown that the channels in this region contained small-scale rivers approximating the size of the present Musselshell River, a river about 15 m wide and with a maximum depth of a couple of meters.

Methods and Materials

Approximately 3,000 specimens have been recovered from the quarries within this region. All six quarries were excavated while screenwash operations (a procedure for bulk washing of sediment and well-known from recovering such very small fossil remains as mammal teeth, fish denticles, etc.; see Hibbard, 1949, or McKenna, 1962, 1965) were performed extensively at Careless Creek Quarry and Top Cat Quarry and to a much lesser degree at Antelope Head Quarry. These operations have provided evidence of a diverse fauna. The remains of various fishes, crocodiles, turtles, champsosaurs, pterosaurs, hadrosaurine and lambeosaurine hadrosaurs, ceratopsians, ankylosaurs, pachycephalosaurs, carnosaurs, coelurosaurs, and multituberculate and marsupial mammals comprise the range of taxa collected so far. Records of the occurrences of each taxon at each quarry are provided in Table 1, while the left margin records the faunal list for the entire region. The quarries are listed across the top of the table as they occur along an approximate east-west transect in the field (Figures 1, 2). The specimens have been identified to genus where possible and in all other cases they have been identified down to the most precise taxonomic level possible.

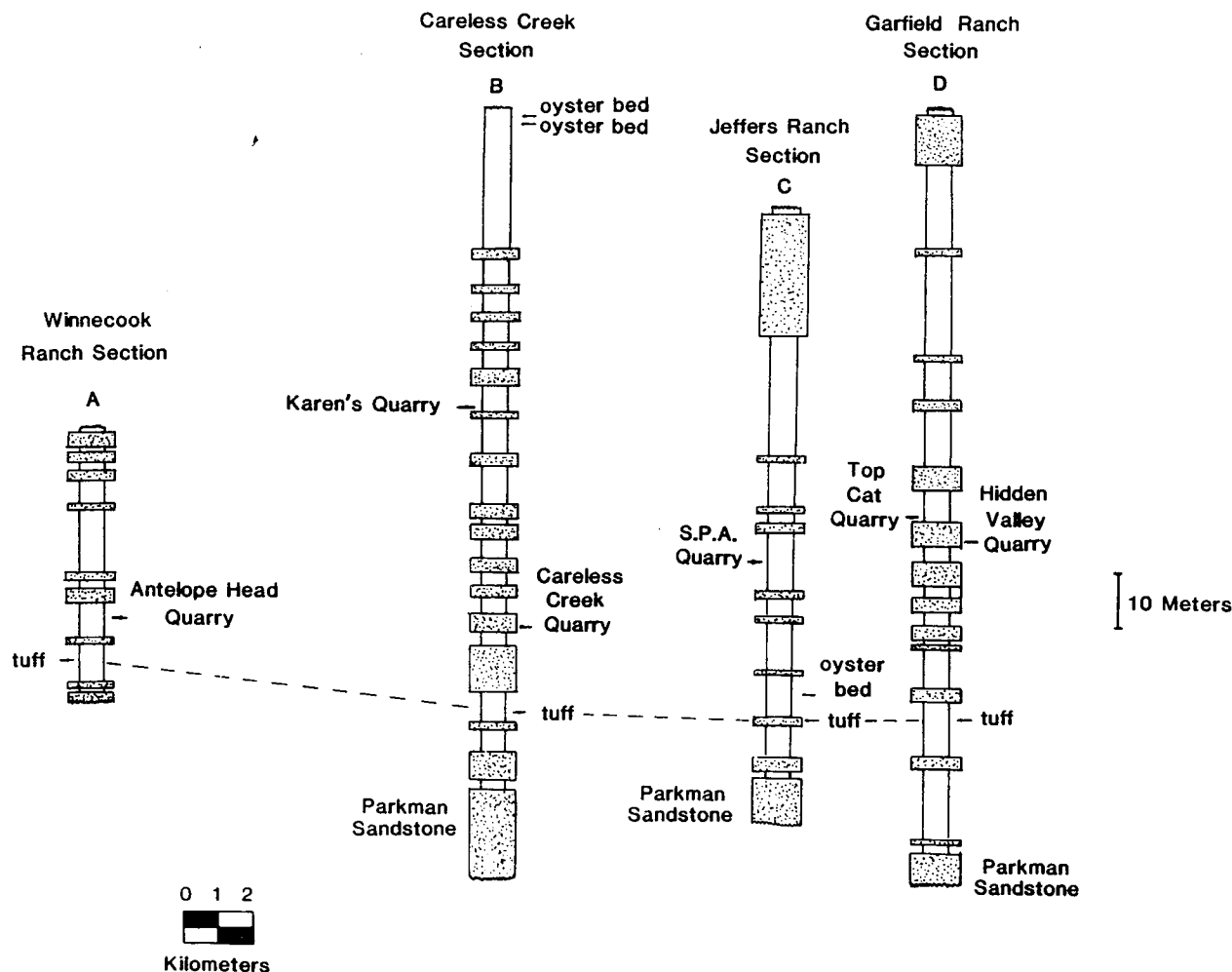


Figure 2. Stratigraphic sections showing the relative position of fossil quarries. Note the abundance of fine mudstones (blank regions) compared to the sandstones (dotted regions) in each section. The letters A, B, C, and D correspond to the labeled positions in Figure 1.

The Fauna

Fishes

The fish fauna from these quarries is among the richest of the material recovered. By far the most abundant fish taxon recovered is the ray *Myledaphus*, represented by hundreds of isolated teeth. This ray is typically considered to be a freshwater taxon (e.g., Estes & Berberian, 1970; Breithaupt, 1982), but is ubiquitous with respect to its occurrences in the faunal facies of the quarries discussed here. Among the other elasmobranch fishes present are the much less abundant rays *Protoplatyrhina* and *Ischyrhiza*, recognized from a few dermal denticles. The sharks *Hyobodus*, *Odontaspis*, and *Eucrossorhinus* are represented by an assortment of denticles and teeth and provide the most reliable environmental information from the cartilaginous fishes. Shark diversity has been used to determine the relative position of fossil sites to the ancient shoreline in the Late Cretaceous Hell Creek Formation of Montana (Estes et al., 1969). The diversity of sharks at the eastern quarry, Top Cat Quarry (Table 1), is similarly an indication of closer proximity

to marine waters than the westernmost quarries such as Careless Creek Quarry.

The osteichthyans, or bony fishes, are also well represented at these new quarries. Present, although uncommon, are the sturgeon *Acipenser* and the bowfin *Kindleia*. The modern amiids, or bowfins, are freshwater fishes, while modern sturgeons are found in both fresh and brackish water (Howes, 1985). The sturgeon remains discussed here are included among the brackish-water fishes.

Belonostomus, the long-snouted chondrosteian, has been recovered only from Careless Creek and Top Cat Quarries; it is generally considered to be a marine fish (e.g., Estes & Berberian, 1970; Sahni, 1972). Case (1978), however, lists *Belonostomus* as a freshwater teleost but provides no arguments for his view, which may be suspect since it appears that this view is meant as a paraphrasing of Sahni (1972; see Case, 1978, p. 178). It is difficult to envision elements of the marine fauna being reworked upstream since sediment transport in a fluvial system is largely downstream. Therefore, based on the distribution of *Belonostomus* in the quarries discussed here, this fish is included among those which inhabited brackish water. Alternatively, it may be that these few specimens represent reworking of the underlying

Table 1.

Faunal list of taxa recovered from new quarries in the Judith River Formation of south-central Montana. The quarries are listed as they approximately occur along an east-west transect. X's designate the occurrence of a taxon at a particular quarry.

Taxa	Quarry					
	AHQ	CCQ	KQ	SPAQ	HVQ	TCQ
Order Ctenacanthiformes						
Family Hybodontidae						
<i>Hybodus</i>						X
Order Euselachii						
Family Synechodontidae						
<i>Eucrossorhinus</i>						X
Order Galeomorpha						
Family Carchariidae (Odontaspis)						
<i>Odontaspis</i>						X
Order Batoidea						
Family Rhinobatidae						
<i>Protoplatyrhina</i>						X
Family Sclerorhynchidae						X
<i>Ischyrrhiza</i>						X
Family Chimaeridae						X
<i>Myledaphus</i>		X				X
Order Acipenseriformes						
Family Acipenseridae						
<i>Acipenser</i>		X			X	X
Order Lepisosteiformes						
Family Lepisosteidae						
<i>Lepisosteus</i>		X	X			X
Order Amiiformes						
Family Amiidae						
<i>Kindleia</i>						X
Order Aspidorhynchiformes						
Family Aspidorhynchidae						
<i>Belonostomus</i>		X				X
Order Elopiformes						
Family Phyllodontidae						
<i>Paralbula</i>		X			X	X
Teleost, indeterminate				X		X

Table 1, continued.

Taxa	Quarry					
	AHQ	CCQ	KQ	SPAQ	HVQ	TCQ
Order Urodela						
Family Batrachosauroididae						
<i>Opisthotriton</i>						X
Family Scapherpetonidae						
<i>Scapherpeton</i>						X
Order Chelonia						
Family Baenidae						
<i>Boremys</i>		X				X
<i>Neurankylus</i>		X				
Baenid, indeterminate		X			X	
Family Dermatemydidae						
<i>Basilemys</i>	X					
Family Trionychidae						
<i>Aspideretes</i>	X	X	X	X	X	X
Order Choristodera						
Family Champsosauridae						
<i>Champsosaurus</i>	X	X				X
Order Squamata						
cf. Infraorder Diploglossa						X
Order Crocodylia						
Ziphodont crocodilia						
cf. <i>Doratodon</i>		X				
Family Alligatoridae						
<i>Brachychampsia</i>		X				
Family Crocodylidae						
<i>Leidyosuchus</i>	X	X				X
Order Pterosauria						
Family Azhdarchidae					X	
Pterosaur indeterminate		X				
Order Saurischia						
Family Ornithomimidae		X			X	
Family Elmsauridae						
<i>Chirostenotes</i> "A"		X				
<i>Chirostenotes</i> "B"		X				
Family Dromaeosauridae						
<i>Dromaeosaurus</i>		X				
<i>Saurornitholestes</i>		X				X
Family Saurornithoididae						
<i>Troodon</i>	X	X				
Carnosaur "A"	X	X				X
cf. Family Tyrannosauridae	X	X				

Table 1, continued.

Taxa	Quarry					
	AHQ	CCQ	KQ	SPAQ	HVQ	TCQ
Order Ornithischia						
Family Hadrosauridae						
<i>Kritosaurus/Hadrosaurus</i>		X				
<i>Corythosaurus</i>		X				
<i>Parasaurolophus</i>		X				
Hadrosaurine, indeterminate	X	X			X	
Lambeosaurine, indeterminate		X				
Hadrosaur, indeterminate	X	X	X			X
Family Pachycephalosauridae						
<i>Stegoceras</i>	X	X	X			
Family Ankylosauridae						
<i>Euoplocephalus</i>		X				
Ankylosaur, indeterminate		X				X
Family Ceratopsidae						
<i>Centrosaurus/Monoclonius</i>		X		X		
<i>Avaceratops</i>		X				
cf. <i>Chasmosaurus</i>	X					
Ceratopsian, indeterminate		X	X			
Order Multituberculata						
Family Neoplagiaulacid						
<i>Mesodma</i>		X				X
Order Marsupialia						
Family Didelphidae						
<i>Alphadon</i>						X
Family Stagodontidae						
<i>Eodelphis</i>						X

marine units during the Judithian. Since no taphonomic distinction, such as color differences, increased abrasion on the *Belonostomus* specimens, or in fossilization, can be made between these specimens and the rest of the fossil assemblage, this scenario seems unlikely.

The other bony fishes recovered are the albulid, *Paralbula*, represented by isolated teeth and tooth plates, and the gar-fish, *Lepisosteus*, represented by abundant scales. *Paralbula* teeth are much more common in the easternmost quarries (Top Cat and Hidden Valley Quarries) than are Careless Creek Quarry, the only other quarry which has yielded specimens belonging to this taxon. This fish is characterized by its button-like teeth which are arranged into large tooth pavements. Although Estes (1969) has suggested that all phyllodontid fish, which includes *Paralbula*, lived near shore or were reef fishes subsisting on a diet of hard-shelled invertebrates, Case (1978, p. 178), again, lists this fish as a freshwater teleost. Modern *Lepisosteus* are

found in either fresh water or brackish water (Howes, 1985). For this study they are considered to be dominantly brackish-water fishes.

Amphibians

The remains of amphibians are somewhat rare from these quarries in comparison with similarly sized fish material. A few fragments of skeletal material can be attributed to the salamander *Scapherpeton* and a few vertebrae of the salamander *Opisthotriton* have also been recovered from Top Cat Quarry. This paucity of material may be result of the ancient environment or may be due to the degree of recognizability of skeletal elements of salamanders, compared to fishes, may have when they are broken. Estes (1964, p. 157) used a similar line of reasoning, though due to modern weathering alone, to account for the poor

representation of material from the amphibian *Prodesmodon* from one of his localities in the Lance Formation.

Champsosaurs

Champsosaurs are crocodile-like aquatic reptiles that are reasonably common in Late Cretaceous to Early Tertiary rocks in the northern hemisphere. These animals ranged in size from less than a meter to several meters in length (Langston, 1958). The long, slender, gavial-like jaws of these animals suggests that they were fish-eaters similar to phytosaurs and ichthyosaurs (Russell, 1956). Historically, these animals have been considered to be freshwater dwellers (e.g., Romer, 1966), but more recently it has been recognized that some of these animals may have had brackish-water or near-marine affinities (Erickson, 1972, 1987).

Champsosaur remains are fairly uncommon at all of the quarries. Vertebrae are the most common such remains found, while teeth, ribs, and appendicular skeletal elements are rare.

Turtles

The quarries are rich in turtle remains, although skulls have not yet been found. Included within the turtle remains are several complete or nearly complete large trionychid, or soft-shelled turtle, carapaces measuring up to 600 mm in length (Figure 3A), with less complete plastra; a *Boremys* plastron (Figure 3B) and partial carapace; several other baenid plastra; and well preserved limb and girdle material referable to both baenids and trionychids. Trionychid axial elements are rare, yet trionychids dominate the turtle fauna. Other turtle genera from these quarries are *Neurankylus* and *Basilemys*.

The authoritative work by Gaffney (1972) describes *Boremys* and *Neurankylus* as baenids, and as recently as 1986 Hutchison & Archibald placed *Neurankylus* within the Baenidae, but Carroll (1988) lists both taxa as neurankylids, a family belonging to the superfamily Baeniodea. *Basilemys* is a member of the family Dermatemydidae, which Hutchison & Archibald (1986) consider to be a "wastebasket" taxon.

The inferred habitat for both trionychid and baenid turtles is aquatic, while further speculation on baenid habitat preference suggests that baenids were generally bottom-dwellers preferring active channel environments (Hutchison & Archibald, 1986). *Basilemys*, in contrast, preferred a terrestrial habitat, was herbivorous, and tortoise-like in appearance (Hutchison & Archibald, 1986). Although the turtle-eating alligator *Brachychampsia* (Carpenter & Lindsey, 1980) is present at Careless Creek Quarry, no tooth damage from this animal was observed on any of the turtle shells recovered.

Lizards

As with the amphibians, there is a marked lack of lizard remains from these quarries. One jaw fragment, the anterior portion of a left dentary, has been recovered from Top Cat Quarry but it lacks many of the features needed to allow a generic identification. Due to its robust nature and closely packed anterior-posterior compressed teeth this specimen may belong to the

infraorder Diploglossa and perhaps even to the family Anguidae (Breithaupt, personal communication).

Crocodyles

The crocodile remains from these quarries are largely isolated teeth although a few vertebrae, scutes, and other assorted materials have also been recovered. By far the dominant crocodilian is *Leidyosuchus*. The alligator *Brachychampsia* is also present but in much smaller numbers. An unusual rare crocodilian is a ziphodont (dinosaur-like) crocodile represented by a single tooth (ANSP 16246). Ziphodont crocodile teeth have been well documented in South America (e.g., Simpson, 1937; Colbert, 1946) and had for sometime confused workers into believing dinosaurs had lived into the Tertiary on that continent (see Simpson, 1932, for discussion). The ziphodont crocodiles from south America belong to the family Sebiciidae of the suborder Mesosuchia (Carroll, 1988). Langston (1956) suggested this taxon was a cosmopolitan group of crocodiles since ziphodont crocodile teeth are recognized from other continents. This claim was later retracted by Langston (1975) upon the realization that many ziphodont crocodiles belong instead to the suborder Eusuchia. Although Molnar (1978) assigned all ziphodont crocodile teeth from the Upper Cretaceous of the northern hemisphere to the genus *Doratodon*, a mesosuchian crocodile, Carroll (1988) lists the genus as occurring only in the Upper Cretaceous of Europe, but provides no explanation.

Pterosaurs

Pterosaur material recovered has been extremely fragmentary, and only two quarries have produced any unequivocal remains--Careless Creek Quarry and Hidden Valley Quarry. In each quarry the yield has only been one bone but in both instances the specimens can be identified as limb elements. The specimen from Hidden Valley Quarry (ANSP 16464) has been recognized as the third wing phalanx of a large pterosaur that shares some characteristics with *Quetzalcoatlus* and is certainly not *Pteranodon* (C. Bennett, written communication, 1987). Although initially described from late Maastrichtian beds, *Quetzalcoatlus* has been tentatively assigned to the fauna from the Judith River Formation of southern Alberta (Currie & Russell, 1982) and it may be the taxon to which ANSP 16464 is assignable (C. Bennett, written communication).

From a time-equivalent rock unit, the Two Medicine Formation of Montana, Padian (1984) recently described the remains of a large pterodactyloid pterosaur, which is not meaningfully compared to either *Pteranodon* or *Quetzalcoatlus*. He then erected the pterosaur families Titanopterygiidae and Pteranodontidae. The former taxonomic unit was later changed to the family Azhdarchidae (Padian, 1986), a modification of Nessov's (1984) subfamily Azdarchinae.

Dinosaurs

There are several aspects of the dinosaur fauna recovered thus far which are noteworthy. The Careless Creek bonebed has been the major focal point of much of the earlier work carried out by the field parties from the Academy of Natural Sciences/Univer-

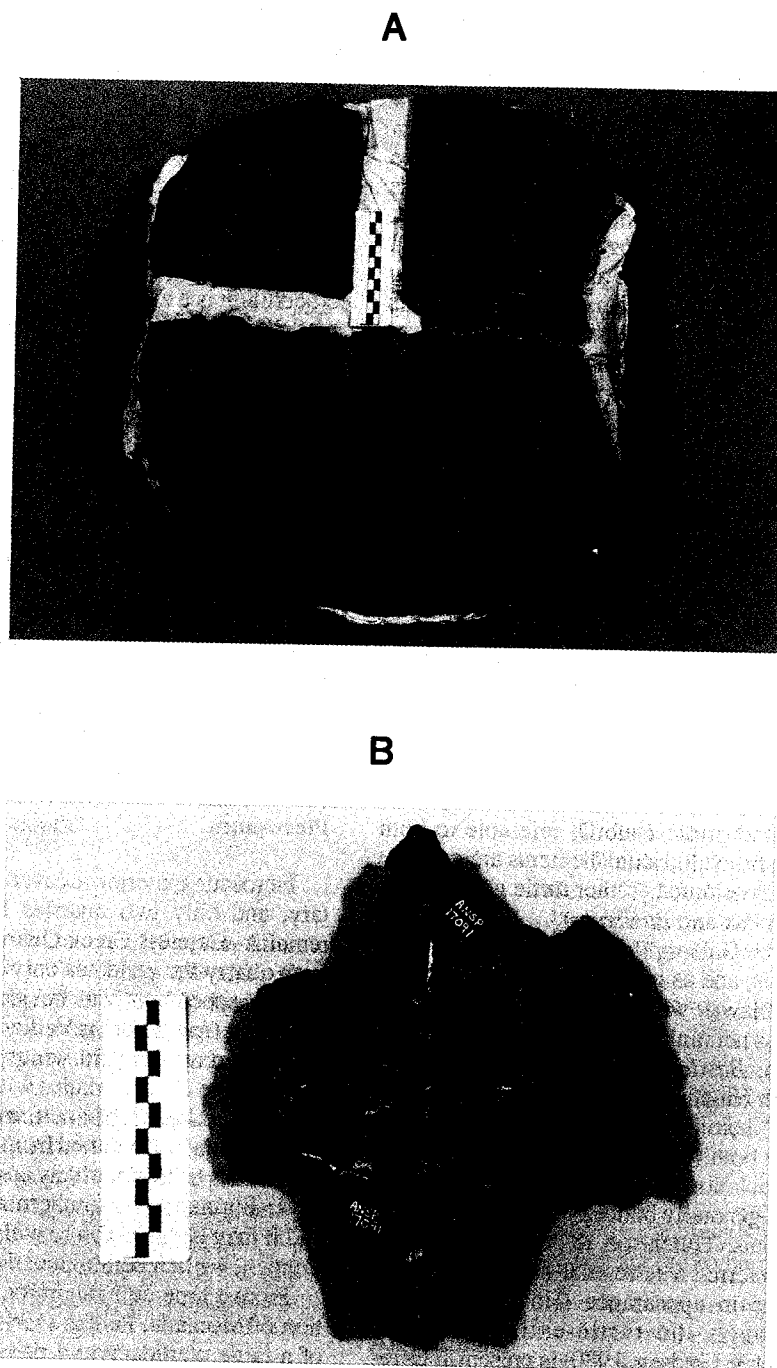


Figure 3. A, *Aspidosaurus* carapace (ANSP 17090), dorsal view, from Careless Creek Quarry, Judith River Formation, Wheatland County, Montana. B, *Boremys* plastron (ANSP 17091), ventral view, from Careless Creek Quarry. Scale bars are 10 cm.

sity of Pennsylvania (Dodson, 1986; Fiorillo, 1987a, in prep.). This quarry has been proven to be the southernmost productive dinosaur site in the Judith River Formation. Thorough sampling of both the Careless Creek Quarry and the surrounding region has shown that although the Judith River Formation of south-central Montana contains faunal elements which can be found in

the northern distribution of the formation, the southern Judith River beds also contain faunal elements which are distinct from the faunas of the northern Judith River beds.

Careless Creek Quarry has yielded a disarticulated, but associated, partial skeleton of the new centrosaurine ceratopsid, *Avaceratops lammersi* Dodson, 1986, a ceratopsid which is as

yet unknown from any other location. The westernmost site within our series of quarries (Antelope Head Quarry) yielded a gigantic hadrosaur femur (ANSP 16466) which measures approximately 1300 mm, the length of the femur of *Tyrannosaurus rex*. For comparison, the femur length of typical Judithian hadrosaurids is 1000 to 1050 mm, and the maximum recorded by Lull & Wright (1942) is 1140 mm, that of *Kritosaurus notabilis*. Also, Morris (1981) described a new species of *Lambeosaurus*, *?L. laticaudus*, from Baja California, which has a femur length of approximately 1280 mm. This new femur is clearly among the longest known for the Judithian.

In addition to the above, a number of small and large theropod teeth (N = 14) have been recovered from three quarries that prove, on close examination, to be other than tyrannosaurid. In fact, they share many of the features of teeth from allosaurids (Currie & Fiorillo, in prep.). It is unlikely that these teeth are from allosaurids since this family is unknown beyond the Lower Cretaceous, and is definitely not known to occur in the better-sampled Judith River Formation of Alberta (Currie & Fiorillo, in prep.). These teeth are referred to in Table 1 as carnosaur "A." These dinosaur occurrences suggest that a distinct dinosaurian biogeographic community exists in the Judith River of southern Montana separate from the Judith River of northern Montana and southern Alberta. Lehman (1987) documented three diverse dinosaur communities in the Late Maastrichtian of the western interior of North America which he attributed to adaptation to a "deteriorating" climate at the very end of the Cretaceous. The data presented here may indicate this faunal response to climatic change began as early as the Campanian, or that lateral biozonation of dinosaur communities was more prevalent than had been previously considered. Further sampling in the region discussed here is needed, however, before full acceptance of the existence of this biogeographic community is possible or to determine if the community differences are limited only to the dinosaur fauna.

These sites have also yielded previously recognized, but rare, taxa as well as fossils of juvenile animals. Most notable among the rare taxa, perhaps, are the pachycephalosaurids which are a group of enigmatic dinosaurs characterized by thickened, domed heads. Only a single skull and associated skeleton has been discovered in North America (Gilmore, 1924) although isolated fronto-parietals are relatively common (Chapman et al., 1981; Dodson, 1983; Sues & Galton, 1985; Giffin et al., 1987). In contrast, greater taxonomic diversity of pachycephalosaurids occurs in the deposits of China and Mongolia (Maryanska & Osmolska, 1974; Perle et al., 1982). Even here, however, only a few postcranials have been described. Pachycephalosaurid postcranialia from Careless Creek Quarry include an ischium, a femur (Figure 4A), and a vertebra. These discoveries are significant since they are, apparently, only the second North American report of pachycephalosaurid postcranialia. Teeth attributable to cf. *Stegoceras* were also recovered from Careless Creek Quarry.

Careless Creek Quarry has also with regularity yielded the remains of juvenile and small dinosaurs; about 20 percent of the 600 dinosaur specimens recovered belong to juveniles (Figures 5A, 5B). This yield of juvenile dinosaur remains is unprecedented outside of the celebrated dinosaur nurseries of northwestern Montana (Horner & Makela, 1979; Horner, 1982,

1984, 1987). For instance, juveniles are between one and two orders of magnitude more common at the Careless Creek Quarry than they are at Dinosaur Provincial Park in Alberta (Dodson, 1983). The discoveries of juvenile dinosaurs at Careless Creek Quarry call into question the idea that dinosaur breeding was confined to upland areas (Sternberg, 1955; Horner, 1982, 1984, 1987; criticized by Carpenter, 1982; Fiorillo, 1987a). Juvenile dinosaur remains are by no means restricted to Careless Creek Quarry. Small hadrosaur teeth and a juvenile ornithischian maxilla fragment (ANSP 16455) have been recovered from Top Cat Quarry and a worn juvenile fragment is known from Antelope Head Quarry (ANSP 16456).

Hadrosaur remains are extremely abundant in most Upper Cretaceous dinosaur localities. In the absence of skull material, generic identification of hadrosaur material is difficult. Brett-Surman (1972), however, recognized generic differences in hadrosaur post-crania, most notably the pelvic bones, in hadrosaur type specimens. There is an abundance of hadrosaur post-crania recovered from the Careless Creek Quarry, particularly illia and pubes, with fewer ischia. Comparison of the Careless Creek Quarry material with the data provided by Brett-Surman (1972) shows that *Kritosaurus-Hadrosaurus* is the dominant hadrosaurine hadrosaur at the quarry. Also present at the Careless Creek Quarry are lambeosaurine hadrosaur post-crania which appear to represent the remains of two lambeosaurs, *Parasaurolophus* and *Corythosaurus*. Although the juvenile hadrosaurs from the quarry have been identified as lambeosaurine (Fiorillo, 1987a), the hadrosaur pelvic remains from the site are all of adult proportions so generic identification of the juvenile hadrosaurs is not directly available. Even if these elements were present at the quarry, potential changes in the dimensions of the pelvic bones during growth are likely to render Brett-Surman's criteria inappropriate. (In the case of *Maiasaura*, however, the post-cranials of the nestlings mimic the morphology of the post-cranials of the adults; Baird, written communication, 1988). It is tempting to speculate, however, that since it has been shown that hadrosaurs are capable of sophisticated adult-nestling/yearling interactions (e.g., Horner, 1984), the presence of either *Parasaurolophus* or *Corythosaurus* adults with such small lambeosaurine hadrosaurs may be an indication of the generic identity of the juveniles.

In addition to the remains of the various dinosaur taxa discussed above, these quarries have also yielded numerous chasmosaurine and centrosaurine ceratopsian remains (Figure 4B).

Mammals

Screenwashing has produced mammal teeth from two quarries, Careless Creek Quarry and Top Cat Quarry. Although the total sample size is small (N = 8), the list of mammals represented includes at least one multituberculate mammal, *Mesodma*, and two marsupial mammals, *Alphadon* and *Eodelphis* (Table 1).

Interpretation of the Fauna

Careless Creek Quarry (CCQ) and Top Cat Quarry (TCQ) have produced by far the most taxonomically diverse faunas, and these two quarries will form the basis for most of the detailed

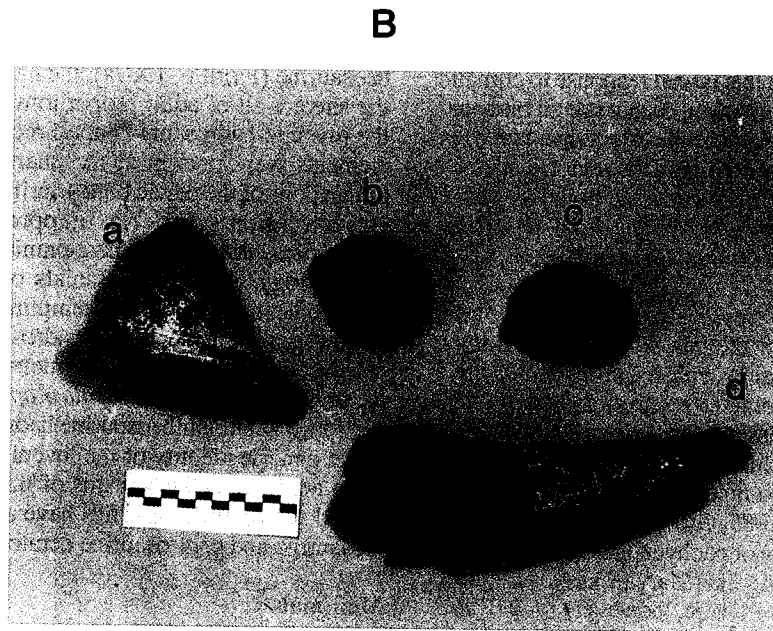
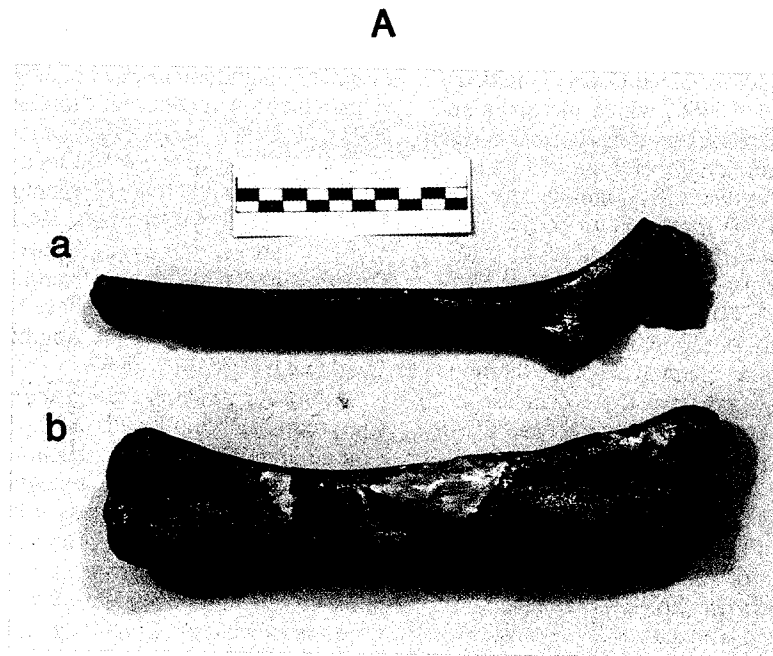
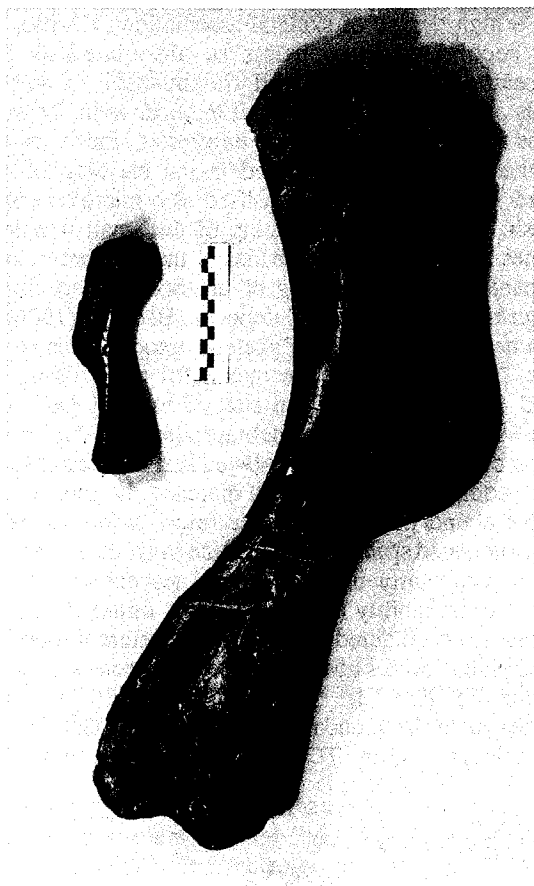


Figure 4. Aa, Pachycephalosaur ischium (ANSP 16987) from Careless Creek Quarry, Judith River Formation, Wheatland County, Montana. Ab, Pachycephalosaur femur (ANSP 16986) from Careless Creek Quarry. Ba, Centrosaurine (cf. *Centrosaurus*) orbital horn core (ANSP 17092) from near Careless Creek Quarry. Bb and Bc, Ceratopsian occipital condyles from Antelope Head Quarry, Judith River Formation, Wheatland County, Montana (ANSP 16298 and 16297, respectively). Bd, Chasmosaurine (cf. *Chasmosaurus*) orbital horn core (ANSP 16488), from Antelope Head Quarry. Scale bars are 10 cm.

Figure 5. (Facing page.) A, Adult lambeosaur humerus (ANSP 15981) and juvenile lambeosaur humerus (ANSP 15979) from Careless Creek Quarry, Judith River Formation, Wheatland County, Montana. B, Adult lambeosaur scapula (ANSP 15981) and juvenile lambeosaur scapula (ANSP 15979) from Careless Creek Quarry. Note that the juvenile elements are approximately one-third the length of the adult elements. This percentage corresponds well with the percentage of adult-size juvenile maiasaurs that have been found still associated with their nests (Horner, 1982). This suggests that these individuals were not far from their nesting areas and that the adults were nesting in a coastal lowland environment (Fiorillo, 1987a), contrary to the generally held view of dinosaur nesting being confined to upland areas (cf. Horner, 1984). C, Adult lambeosaur maxilla (ANSP 15981) and dentary (ANSP 15981) from Careless Creek Quarry. D, Selected adult hadrosaur vertebrae and chevrons from Careless Creek Quarry: Da, ANSP 16831; Db, ANSP 16824; Dc, ANSP 16830; Dd, ANSP 16823. Scale bars are 10 cm.

A



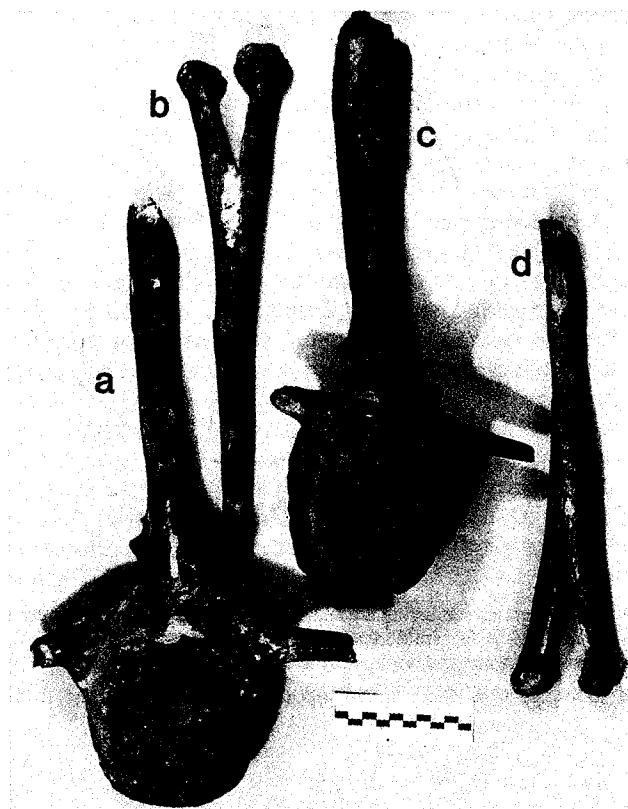
B



C



D



quarry comparisons. Figure 6 illustrates the generic differences between TCQ and CCQ. Most noticeable is the increase in marine/brackish-water fish taxa in the easternmost quarry, TCQ, and the increase in the number of dinosaur taxa at the western CCQ. This difference in fish taxa is attributed to the closer proximity of TCQ to the ancient shoreline compared to CCQ. The greater abundance in dinosaur taxa at CCQ may be, in part, an artifact of the abundance of diagnostic postcranial material providing opportunity to diagnose more genera there than at TCQ. Although larger dinosaur elements (e.g., unguals) have been recovered from fine-grained deposits of TCQ, these deposits may be indicative of a fluvial system which was incapable of transporting many larger dinosaur materials.

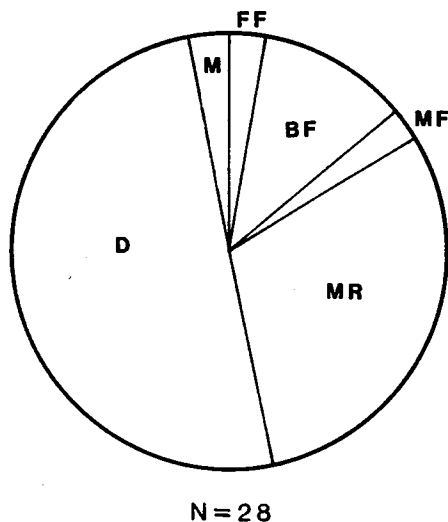
While the diagrams in Figure 6 illustrate the taxonomic differences at each quarry, they do not help demonstrate the differences in relative abundances of faunal elements at the two localities. Methods for computing relative abundances of faunal material at a site as a reflection of the paleoenvironment have varied (e.g., Klein & Uribe-Cruz, 1984; Grayson, 1984). Badgley (1986) has argued that within the channel deposits of the Late Tertiary to Pleistocene Siwaliks of Pakistan, where specimens have low probabilities of association, relative abundances of individual animals at a site can be estimated by using the number of identifiable specimens at a site (NISP). At CCQ, a channel deposit, it can be shown that although many of the bones at the site can be treated in this manner, a second subset of bones is more effectively treated by using minimum number

of individuals (MNI) for estimating faunal abundance since they have a high degree of skeletal association (Fiorillo, in prep.). This second subset consists of associated skeletons of hadrosaurs, ceratopsians, and trionychids. Combining the results of the NISP and the MNI methods is the most effective means for determining relative numbers of individuals at CCQ, and these results are presented in the pie diagram shown in Figure 7A. TCQ can be classified as a microvertebrate fossil deposit; that is, a site consisting of the small remains of vertebrates in contrast to large bones of the vertebrate skeleton, an overbank deposit consisting of unassociated specimens. Although referring to channel deposits, Badgley (1986) suggests that when the probability of skeletal association is negligible at a site, NISP is an effective means for determining relatively faunal abundance at a fossil site. Similarly, Dodson (1987), while working with microvertebrate sites in the Judith River Formation of southern Alberta, showed that the census totals of the faunal components of his sites matched, in general terms, the relative abundances of the same faunal components obtained from articulated specimens within the same formation. This pattern is particularly noticeable with respect to the dinosaurs. Since the probability of association is minimal at TCQ, each specimen is considered to belong to a different individual; and the relative numbers of taxa for the quarry are shown in the pie diagram in Figure 7B.

Because of the abundance of *Myledaphus* teeth and *Lepisosteus* scales at CCQ and TCQ, census results for these taxa should

TAXONOMIC DIVERSITY

CARELESS CREEK QUARRY



TOP CAT QUARRY

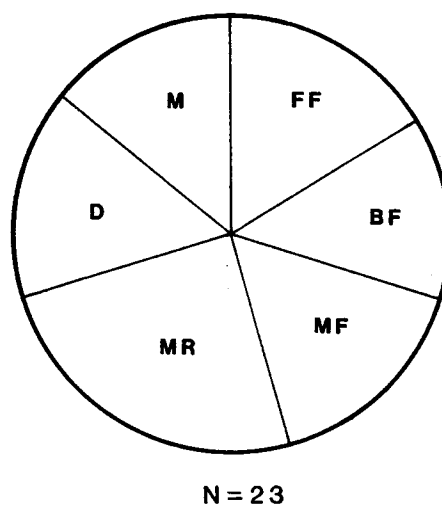
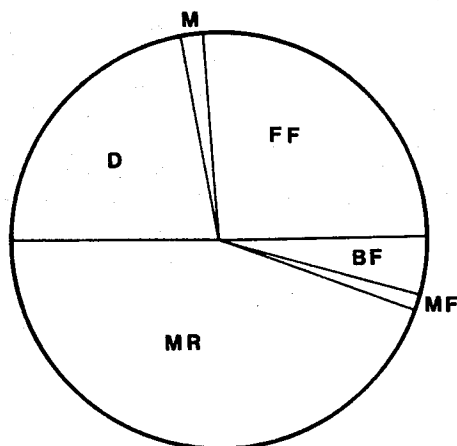


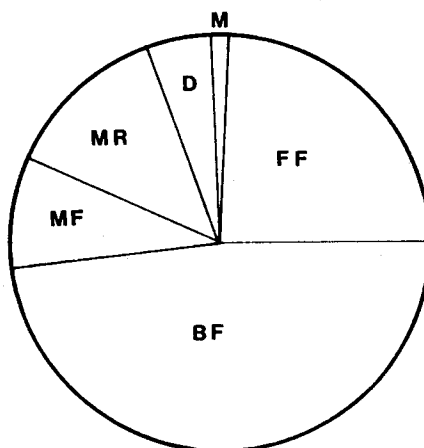
Figure 6. Pie diagrams comparing the taxonomic diversity of Careless Creek Quarry and Top Cat Quarry. Abbreviations: FF (freshwater fish), BF (brackish-water fish), MF (marine fish), MR (mesoreptiles), D (dinosaurs), and M (mammals). Mesoreptiles are comprised of all non-dinosaurian reptiles. Notice the increase in the number of brackish-water and marine fish taxa at Top Cat Quarry compared to Careless Creek Quarry. Also note the abundance of dinosaur taxa at CCQ compared to TCQ.

RELATIVE ABUNDANCE

CARELESS CREEK QUARRY



TOP CAT QUARRY



ie diagrams comparing the relative abundances of fossil remains at Careless Creek Quarry and Top Cat Quarry. Abbreviations are the same as those used Mesoreptiles are comprised of all non-dinosaurian reptiles. Notice the increase in abundance of brackish-water and marine fishes at Top Cat Quarry compared to Careless Creek Quarry.

cautiously. For example, if an animal has a large number of skeletal elements which are diagnostic of the taxon, but the elements offer no indication of having been derived from a single individual, the possibility of inflating the ecological significance of that taxon must be considered. A gar, for example, includes many preservable scales as part of its skeleton. Finding one of such fish near a site at the time it is forming can contribute hundreds of scales without providing a clue that they came from one individual, leading one to conclude that garfishes were plentiful at that time and place. Similarly, Dodson (1987) reports an anomalous occurrence of abundant dermal ossicles at a microvertebrate locality in the Judith River Formation of southern Alberta. This is most likely the result of the carcass of an ankylosaur nearby or a contribution to the site of a coprolite from a scavenger which contained hundreds of ankylosaur dermal ossicles. Obviously, data from many microsites are needed to serve as a guide to detect relative abundances of taxa. Dodson (1987) provides no numbers for the relative abundances of the taxa *Thrinacosaurus* and *Lepisosteus* but does mention that these are the most abundant fish taxa represented. Likewise, they are so at Top Cat Quarry; therefore the NISP for these taxa are viewed here as a measure of relative abundance at each site.

These data are also problematic for determining relative abundances at a fossil site. Turtles can add fragmented skeletal elements to a fossil assemblage which can inflate their significance in paleoecological reconstructions. The census method used here follows from the conservative method described by Hutchison & Archibald (1986) where, unless there is a distinct difference in an element, an obvious size difference, or a dis-

proportionate amount of material, the smallest possible number of individuals is entered to the census at each quarry.

The relative abundance of brackish-water or marine fishes (Figure 7) greatly exceeds that of freshwater fishes at TCQ, similar to when the taxonomic diversity of these two quarries is compared (Figure 6). The other faunal categories in the relative abundances pie diagram remain consistent with the pattern observed in the diversity diagram for TCQ. The relative abundance diagram for CCQ, however, differs dramatically from the taxonomic diversity diagram for the quarry. Perhaps most significant to the discussion here is the reversal in the pattern of fishes. Whereas at TCQ (Figure 6A) the taxonomic diversity of brackish-water and marine fishes exceeds that of freshwater taxa, the relative abundance of freshwater fishes at CCQ (Figure 7A) exceeds that of brackish-water and marine fishes. A second difference that is observed when comparing both figures is the decline in the relative abundance of dinosaurs. Although the mesoreptiles are represented by large numbers of isolated crocodile teeth and turtle fragments, the number of identifiable specimens for dinosaurs exceeds that for the mesoreptiles. Comparison of Figures 7A and 7B shows that an increase in the relative abundance of brackish-water/marine fishes occurs in TCQ compared to CCQ. As in the diagrams for taxonomic diversity (Figures 6A, 6B), this increase probably reflects closer proximity of TCQ to the paleoshoreline compared to CCQ. This point is corroborated by the increased numbers of oyster beds in the area around TCQ compared to the area around CCQ.

Not all differences observed between faunas, however, should be attributable to an ecological gradient. For example, both sites contain *Myledaphus* teeth (Table 1), the most abundant fish remains at both quarries. The average size of the

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Myledaphus teeth at TCQ is much smaller than at CCQ (Figure 8). The average maximum length of the teeth at TCQ is 0.37 mm (N = 60), while at CCQ the average maximum length is 0.51 mm (N = 60). This increase in average maximum tooth length is approximately 38 percent. The maximum width of the *Myledaphus* teeth was measured perpendicular to the longest dimension (N = 60). The maximum widths of these teeth for TCQ and CCQ were 0.25 mm and 0.36 mm, respectively, an increase of approximately 44 percent at CCQ. Rather than be attributed to ecological differences, such as along a salinity gradient, these differences are best explained by the sedimentological context of each site.

Behrensmeyer (1975) and Korth (1979), based on the settling velocities of bones and theoretical quartz spheres, showed that bones of particular sizes can hydraulically equilibrate with

sedimentary particles of specific sizes in a fluvial environment, such that coarser-grained sediments are likely to entomb larger fossils than finer-grained sediments. This is exactly what is observed with the *Myledaphus* teeth at CCQ and TCQ. CCQ is a coarse- to fine-grained channel sandstone while TCQ is a siltstone overbank deposit. This example illustrates the importance of considering the sedimentological context of a site when interpreting the paleoecology of its fauna. In contrast to the *Myledaphus* example, the presence of sharks at TCQ, and not at CCQ, is likely to be a real ecological occurrence. Many of the sharks' teeth are of similar size and shape as many of the crocodile, dinosaur, and mammal teeth found at CCQ. It is improbable, then, that a sedimentologic winnowing process would selectively remove only the sharks' teeth at CCQ and leave behind the similarly sized teeth of other taxa.

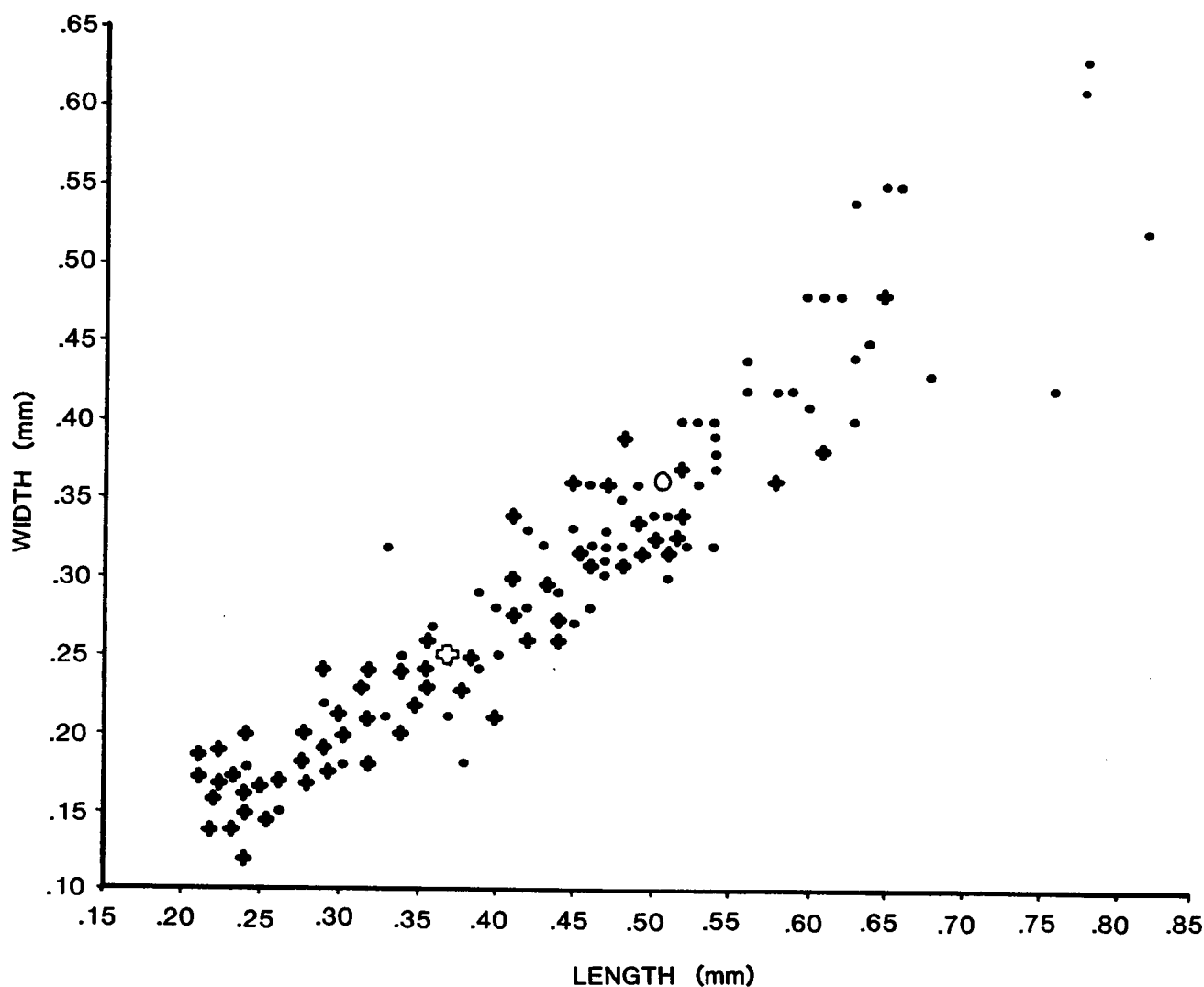


Figure 8. Graph of length-width measurements of 60 randomly chosen *Myledaphus* teeth from Careless Creek Quarry (designated by '+'s) compared to 60 randomly chosen *Myledaphus* teeth from Top Cat Quarry (designated by '•'s). The average of all 60 CCQ measurements is shown by a + and the average of all 60 TCQ measurements is shown by a O. Note the average TCQ *Myledaphus* tooth is larger than the average CCQ *Myledaphus* tooth.

Conclusions

Several dinosaur-producing quarries have been discovered in the Judith River Formation of south-central Montana, an area previously unrecognized for its paleontological significance. These quarries have yielded approximately 3,000 specimens thus far and have provided evidence for a rich and diverse Late Cretaceous vertebrate fauna.

The paleogeographic model for the Late Cretaceous of western North America shows that an epeiric sea lay to the east and tectonically active highlands were to the west. These new quarries are spread out over 25 km in an east-west direction, an appropriate distribution to detect a possible faunal gradient between these two regions. Preliminary sampling of one of the easternmost quarries (Top Cat Quarry) had indeed shown diagnostic features of marine or brackish-water conditions not found, or found in significantly smaller numbers, in the westernmost sites (e.g., Careless Creek Quarry). These indicators include sharks, albulid fishes, and other marine or brackish-water fishes, and also oyster beds at about the same stratigraphic level as the quarries, but were not tied into any sections. These marine or brackish-water indicators are restricted to aquatic taxa, presumably since the distance along this gradient is comparatively insignificant to affect the large terrestrial vertebrates such as the dinosaurs.

The fauna recovered from this region also seems to show differences with the terrestrial dinosaur faunas recovered elsewhere from this formation. More sampling in the Judith River in areas surrounding the present field area is needed to help test if these differences are real.

Acknowledgements

The results presented here are based on data collected from four field seasons of collecting fossils in Montana. During this time a large number of people made significant contributions to the success of each field season. Among them are Sid Hostetter, Nan Dillon, Sue Marsland, Connie Barut, Mark Fiorillo, Cathy Forster, and Brian Forster. Without their help and camaraderie in the field the success of this project would surely have suffered. I also thank Frank Bukowski, Doug Moore, Chuck Smart, Jeff Walker, and Christopher Dodson for their efforts. Peter Dodson provided invaluable assistance both in the field and in the lab. My thanks to him for all of his enthusiastic help. The Lammers family has provided a tremendous amount of logistical support for this project, without which life in the field would have been less bearable. Many of the taxonomic identifications presented in this report were made through the cooperation of others. Drs. Richard Fox, Jason Lillegraven, and J. David Archibald generously identified the mammal teeth from these quarries. Likewise, Drs. Eugene Gaffney and J. Howard Hutchison helped identify the turtle remains. Dr. Donald Brinkman and Brent Breithaupt provided the identifications of the amphibian and lizard remains, and Dr. Phil Currie helped identify the small theropod teeth from these quarries. My thanks to all of them for their time. My thanks also to Dr. Donald Baird and an anonymous reviewer for their helpful reviews of this manuscript. Field work for this project was funded in 1984 by an anonymous donation to the Academy of Natural Sciences of Philadelphia. The 1985 and 1986 field seasons were supported by NSF grant

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